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The vertebrate fauna from Cardamone (Apulia, southern Italy): an example of Mediterranean mammoth fauna

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The site of Cardamone, a karstic cavity in local Plio-Pleistocene calcarenites in the outskirts of Lecce (Apulia, SE Italy), provided a wealthy amount of fossil vertebrates. Although dismembered and partly dispersed in several institutions of Italy, the fauna that survived the vicissitudes of the years is still enormously rich, counting 1886 mammalian specimens and a large amount of bird bones. It includes remains of mammoth (*Mammuthus primigenius*), woolly rhino (*Coelodonta antiquitatis*), aurochs (*Bos primigenius*), red deer (*Cervus elaphus*), horse (*Equus ferus*), wolf (*Canis lupus*), red fox (*Vulpes vulpes*), spotted hyena (*Crocuta crocuta*), hedgehog (*Erinaceus europaeus*), hare (*Lepus europaeus*) and rabbit (*Oryctolagus cuniculus*). This mammal community is suggestive of relatively open landscapes under fairly cold climatic conditions; a picture also corroborated by the avifaunal elements. The fauna from Cardamone seems to be an example of an ecotone wherein typical elements of the *Mammuthus-Coelodonta* faunal complex (*M. primigenius*, *C. antiquitatis*, *E. ferus* and *C. crocuta*) that probably immigrated from the east, are mixed to the more temperate, autochthonous fauna (characterized in particular by *B. primigenius*, *C. elaphus*, *L. europaeus* and *O. cuniculus*). The extensive last Pleniglacial sea-level fall combined to intense late tectonics in the Adriatic area presumably caused the emersion of most of the Adriatic sea-bottom, giving rise to a vast wide open plain which could have acted as a corridor between the Balkan peninsula and the south-eastern regions of Italy, permitting the arrival of the eastern faunal elements. This hypothesis would be consistent with the absence of the *Mammuthus-Coelodonta* faunal complex elements in most of central and southern Italy. An alternative view is the classical one, with the pachyderms following a horseshoe route from the north-east southwards along the Adriatic shores of Italy. Finally, the absence of *E. hydruntinus* and *D. dama* and the presence of *Mammuthus primigenius* and *Coelodonta* may suggest a dating of the assemblage to the climax of the last glacial, that is at the second Würmian Pleniglacial, which is dated some 22-18 ky from present.

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Key words: *Mammuthus-Coelodonta* faunal complex, Late Pleistocene, Apulia, Southern Italy

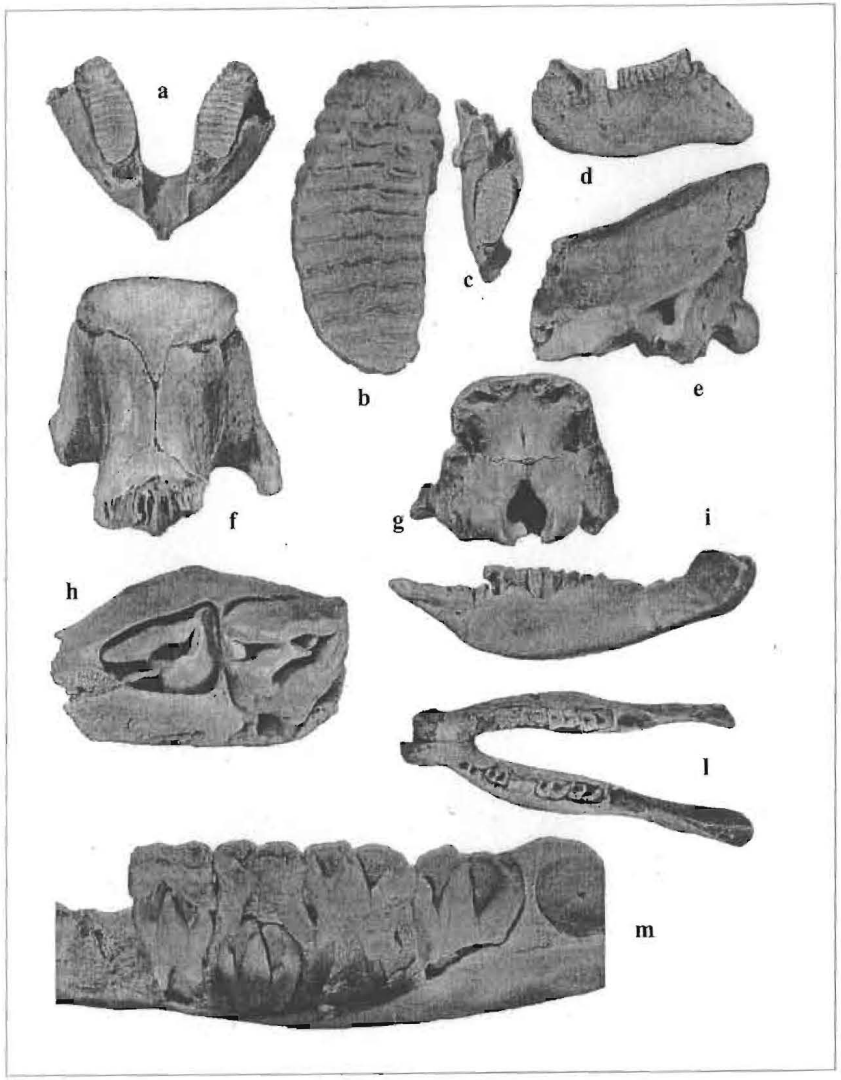

Figure 1 **a-d**: *Mammuthus primigenius* **a**: incomplete juvenile mandible with m1 in function, occlusal view, 1/6 nat. size; **b**: detail of specimen shown in a: left m1, occlusal view, 1/2 nat. size; **c**: incomplete juvenile right hemimandible with d4 in function, occlusal view, 1/6 nat. size; **d**: same specimen shown in c, lateral view, 1/6 nat. size; **e-m**: *Coelodonta antiquitatis* **e**: incomplete juvenile skull, left lateral view, 1/6 nat. size; **f**: incomplete juvenile skull, dorsal view, 1/6 nat. size; **g**: incomplete juvenile skull, occipital view, 1/6 nat. size; **h**: incomplete juvenile right maxillary, with M1 and emerging M2, occlusal view, 1/2 nat. size; **i**: incomplete juvenile hemimandible, left lateral view, 1/6 nat. size; **l**: incomplete juvenile hemimandible, occlusal view, 1/6 nat. size; **m**: incomplete juvenile right hemimandible (detail), lingual view, 1/2 nat. size.

INTRODUCTION

The rich faunal assemblage from Cardamone (Lecce, Apulia, southern Italy) was found in a karstic cavity infilling in local Plio-Pleistocene calcarenites. The cavity was funnel-shaped near the surface and passed to an elongated flue-shaped vertical structure. The latter widened about 15 m below the surface and gave access to a subcircular underground cave about 9 m in diameter. The cave was partly infilled with the same sediment as the vertical cavity, which piled up occluding the entrance to the cave. U. Botti, who is the author of the first report on the fauna (Botti 1890), collected the vertebrates. Subsequent studies were made in the 20th century by Vaufrey (1927), Guérin (1980) and Rustioni (1998). The collection was dismembered over the years and partly dispersed to several institutions of Italy, while other specimens quoted in the literature now seem lost. Unfortunately, this prevented the reconstruction of the original quantitative composition of the fauna and therefore a taphonomic analysis was inhibited. Retracing the bones still preserved in the different institutions was the first concern of the authors. Although depleted, the fauna that survived the vicissitudes of the years is still enormously rich and this makes it very significant from different viewpoints.

MATERIAL AND METHODS

The authors are aware that any possible observation is biased by the unavoidable statistical error represented by the incompleteness of the sample. Yet the impressive abundance of the specimens (1886 mammalian specimens and 70 boxes each containing remains of single bird skeletons) and the fact that practically all the species reported by Botti (1890) are still represented (excluding *Felis*, *Arvicola* and *Mus*), convinced the authors that the fauna was worth considering. The minimum number of individuals (MNI) was thus calculated and deemed to be fairly reliable. The analytical approach adopted here also included the construction of diagrams of bone representation of each species and the observation of bone surface evidence. Most specimens are part of the natural history collections housed by the Istituto Tecnico O.G. Costa, at Lecce. Several others are preserved at the Museo Civico di Paleontologia e Paletnologia di Maglie, in the province of Lecce; a few at the Paleontological and Geological Section of the Museo di Storia Naturale of Florence; an isolated *Mammuthus primigenius* tooth is at the Museo di Paleontologia G. Capellini, at Bologna.

RESULTS

The bones do not show evidence of transportation nor of butchering, scarnification or of other human activity (Fig. 1). Therefore they were not selected under natural circumstances. Diagrams of the bone representation of each species (Figs. 2 - 5) confirm an expected artificial selection of the specimens, possibly

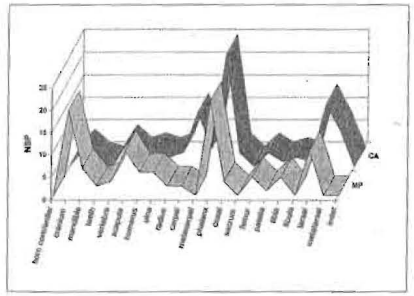

Figure 2 Number of skeletal elements of *M. primigenius* (**MP**) and *C. antiquitatis* (**CA**).

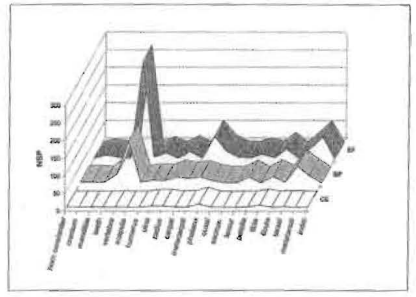

Figure 3 Number of skeletal elements of *E. ferus* (**EF**), *B. primigenius* (**BF**) and *C. elaphus* (**CE**).

Table 1 Minimum number of individuals (juveniles and adults) and number of determined specimens per species.

species	juv	adult	NSP (determined)
M.primigenius	3	0	97
C.antiquitatis	2	0	93
E. ferus	9	29	542
B.primigenius	8	13	321
C. elaphus	1	3	28
C.lupus	7	9	103
V. vulpes	29	58	436
C.crocuta	2	2	26
Mustelidae	0	1	1
E.europaeus	9	0	43
L.europaeus	6	3	73
O.cuniculus	1	1	5
total	77	119	1770

due to both improper recovery (which probably explains the small number of micromammals and of other small vertebrates) and to the following dismembering of the collection. This is particularly evident in the anomalous over- and under-representation of some post-cranial elements with respect to the number of bones expected in conditions of normal accumulation in caves (Table 1, Fig. 6). Noteworthy is the extraordinary high number of red foxes (87 individuals, 29 cubs and 58 adults) in the diagrams depicting the abundance of the different species (Figs. 7 and 8); this may be the result of an attritional accumulation of carcasses over a long time lapse. There are two possible explanations for such an accumulation: (1) the cave was used as a shelter by these animals, which suggests that another entrance originally existed and was later obliterated, or (2) the cave acted as a natural trap. The former hypothesis contrasts with the eco-ethology of these carnivores. Red fox is not a gregarious animal and in normal conditions it does not form groups larger than a female and its cubs. Therefore the large amount of individuals encountered at Cardamone testifies the trapping of single specimens over a long time lapse, although normally these animals are smart enough to avoid a natural trap, especially if fellow specimens fall into it. Assuming that the Würmian red fox formed family groups as large as those living today, the mortality indexes would be determinant in assessing the lapse of time possibly represented in the site. If one applies the mortality indexes calculated in extant red fox populations (Cavallini 1994) the carcasses of these canids present in the Cardamone fauna would have accumulated in some 70 to 80 years. However, these mortality indexes, as those of all European faunas, are heavily biased by the statistical error of also including individuals killed by modern man (specimens shot by hunters, killed by cars, etc.).Incidentally, an interesting trait of the red foxes presently living in the Mediterranean Basin is their genetic structure. Recent researches (Frati *et al.* 1998) have shown that red foxes can be genetically divided into two distinct groups: one includes the representatives from Spain, Sicily, Sardinia and Bulgaria, the other those from peninsular Italy and Austria. This has significant paleogeographic implications

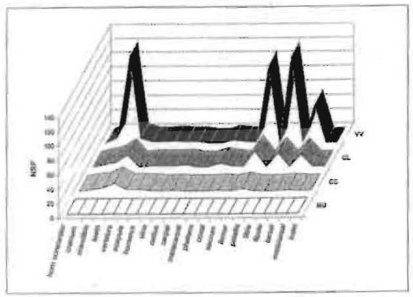

Figure 4 Number of skeletal elements of *C. lupus* (**CL**), *V. vulpes* (**VV**), *C. crocuta* (**CC**) and Mustelidae (**Mu**).

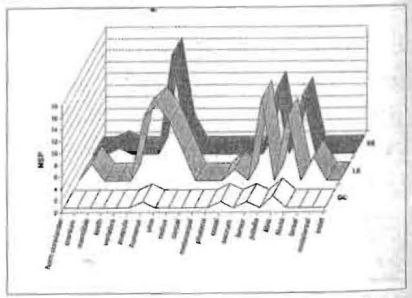

Figure 5 Number of skeletal elements of *O. cuniculus* (**OC**), *L. europaeus* (**LE**), *E. europaeus* (**EE**).

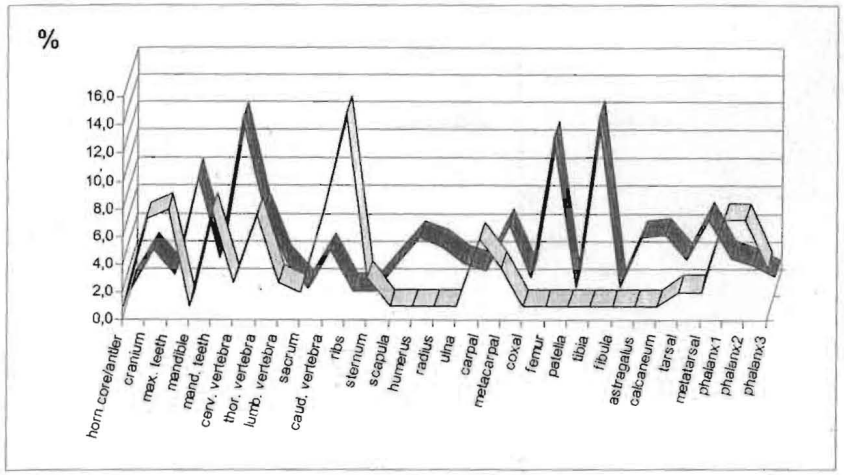

Figure 6 Expected *vs.* actually found abundance of the bone elements from Cardamone. The curve of expected abundance depicts the pattern of relative abundances in an average skeleton. The cranium includes all the main parts it is composed of (occipital, parietal, frontal, etc.). The percentages of specimens are reported on the vertical scale. The diagram is meant to portray the over- or under-representation of bones with respect to the theorical situation in which all bones had been preserved and recovered. Dark grey: expected NSP (%); light grey: observed NSP (%).

which will be analysed more carefully later on.

Besides foxes, the cave provided remains of mammoth (*Mammuthus primigenius*), woolly rhino (*Coelodonta antiquitatis*), aurochs (*Bos primigenius*), red deer (*Cervus elaphus*), horse (*Equus ferus*), wolves (*Canis lupus*), spotted hyena (*Crocuta crocuta*), hedgehog (*Erinaceus europaeus*), hare (*Lepus europaeus*) and rabbit (*Oryctolagus cuniculus*). The percentage of young individuals is very high (Fig. 8); in particular the mammoth and the woolly rhino are only represented by juvenile specimens. The mammalian community as a whole, and the high amount of horse remains (Figs. 7 and 8), seem to be suggestive of fairly open forested steppes. This is apparently consistent with noteworthy absences of some typical representatives of the Late Pleistocene of Italy, such as *Capreolus capreolus*, a characteristic woodland dweller; *Sus scrofa*, a marshy woodland inhabitant; *D. dama*, which however may be lacking for stratigraphic reasons, the Cardamone fauna likely postdating the last occurrence of this species in Europe. Caprine bovids are also lacking, perhaps excluded by the particularly flat physiographic character of the area. At last, the absence of *E. hydruntinus* and, on the other hand, the presence of the woolly rhino and of the mammoth, which substituted the more common *Elephas antiquus* (=*Elephas namadicus*), are suggestive of fairly cold climatic conditions.

The most significant occurrences from the stratigraphical viewpoint are those of the pachyderms, which seem to disperse in Italy during the last glacial (Palombo 1994; Ferretti 1998). The mammoth and, even more, the woolly rhino are extremely rare in Italy and many of the occurrences from Italy reported in the literature are due to misattribution. Scanty remains of both were found in northern and central Italy (a beautiful, but isolated skull of *Coelodonta antiquitatis* was found at Monte Circeo promontory and described by Palmarelli & Palombo 1981) and isolated woolly rhino teeth were recover-

Table 2 Relative abundance in the avifauna.

familiy	specimen
Ardeidae	1
Anatidae	5
Accipitridae	7
Falconidae	1
Otididae	2
Scolopacidae	1
Columbidae	46
Cululidae	1
Strigidae	1
Corvidae	2
other Passeriformes	3

ed in Apulia (Guérin 1980). The two species were never reported from any other part of southern Italy. This find from Cardamone thus confirms the occurrence of the woolly rhino in Apulia and the southernmost known occurrence of the mammoth in Italy.

Cardamone cave also provided a wealthy collection of bird remains (Table 2). Ongoing studies on this material are performed by one of the authors (M. Pavia) and the results of a preliminary analysis can be given here. The avifauna is dominated by the Columbiformes (pigeons), probably *Columba livia*, a bird that lives in caves and on rock cliffs. The presence of water birds, Anatidae (ducks) and Ardeidae (herons), and some birds of prey, *Haliaetus albicilla* and *Circus* sp., seem to indicate an extension of fresh water or lagoons; Otididae (bustards) also indicates open landscapes. The slight amount of small Passeriformes (songbirds) is probably due to improper collecting. The bird remains from Cardamone are not completely representative of the original avifauna of the area; this fact inhibits taphonomic and detailed paleoecological analyses. The preliminary data on the Cardamone avifauna suggest temperate-cold climatic conditions; the environment of the area was probably characterised by an open countryside with scattered wetlands or lagoons not far from the cave.

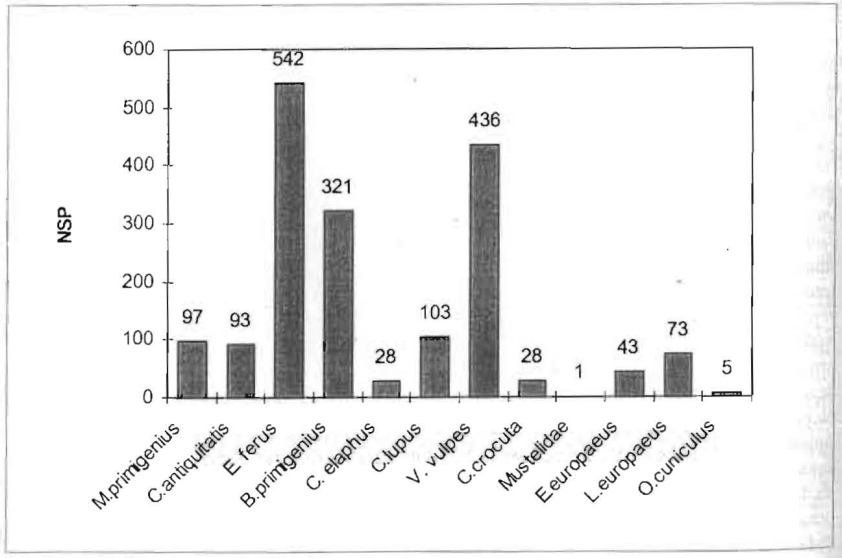

Figure 7 Number of specimens (NSP) per species.

MEDITERRANEAN MAMMOTH FAUNA

Although Chow *et al.*'s (1959) and Kahlke's (1994) Late Pleistocene *Mammuthus-Coelodonta* faunal complex in Italy is slightly and incompletely represented only in the north, single components can also be found in other Italian regions. *Rangifer tarandus* is reported only from Liguria (Palma di Cesnola 1983; Masseti *et al.* 1995); *Alces alces* from Liguria, Veneto and Trentino (Masseti *et al.* 1995); *Megaloceros giganteus* reached central Italy (Pasini 1969, 1970); *Bison priscus* dispersed to Sicily (Masseti *et al.* 1995); *E. ferus* is widely diffused in most of Italy; the carnivores *Canis lupus*, *Ursus spelaeus*, *Panthera leo*, *P. pardus*, *Lynx lynx* and *Crocuta crocuta* are well represented through-out Italy (*C. lupus*, *P. leo* and *C. crocuta* reached Sicily; Bonfiglio and Burgio 1992); *Gulo gulo* was rare. Other steppe taxa not mentioned by Kahlke (1994) are *Ochotona* and *Sicista*, which are reported from Veneto and from the Adriatic side of central Italy (Bartolomei 1980; Sala 1990). *Saiga* and *Ovibos*, on the other hand, never reached Italy.

The occurrence of *Mammuthus* and *Coelodonta* in limited areas of northern Italy, in the central Tyrrhenian side of Italy and in the Salento peninsula, and their absence in most of the Adriatic belt, as well as the over mentioned genetic similarity between red foxes presently living in southern Italy and eastern Europe, may altogether suggest that at the time of the Cardamone fauna the paleogeographic setting was quite different from today. The combination of an extensive sea-level fall and intense late tectonics in the Adriatic area may have caused the emersion of most of the Adriatic sea-bottom, giving rise to a vast wide-open plain which acted as a corridor for the pachyderms of the Balkans to the south-eastern regions of Italy and for red foxes to southern Italy and Sicily. Sea-bottom maps of the Adriatic Basin show an abrupt thickening of the isobaths off the shore-line just north of Pescara and another less marked thickening ENE off the Gargano promontory (Fig. 9). These two step-like structures are

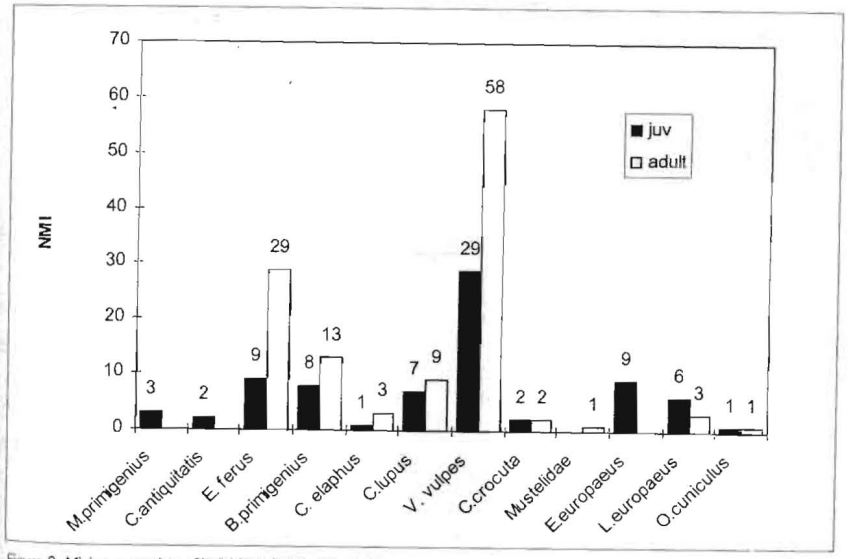

Figure 8 Minimum number of individuals (MNI) per species.

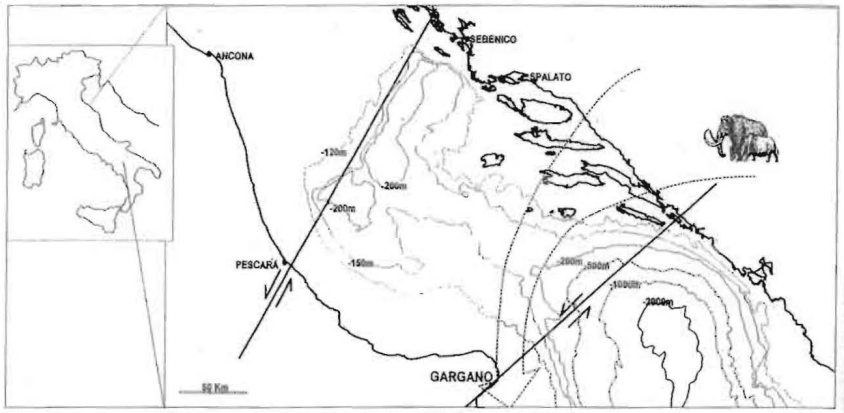

Figure 9 Schematic map showing the -120m to -2000 m bsl isobaths in the Adriatic basin off Pescara and the Gargano promontory; the main SW-NE-trending transform fault systems; one of the suggested ways of immigration of the *Mammuthus-Coelodonta* faunal complex elements towards Apulia (indicated by the wide dotted arrow).

southwest-northeast trending fault systems which lower the sea-bottom from -150 m bsl to about -200 m and -500 m, respectively. These structural lineaments are transform fault systems with a considerable vertical component (dr P. Bettini, pers. comm., 1999). The faults have been active since remote time, but their last intense activation was very recent (possibly even Holocene in age) and they are still very active today. Therefore, in conclusion the possibility of an extensive emerged plain stretched all the way down to Pescara or even farther south to the Gargano promontory, recently disrupted in its southern margin by the mentioned fault systems, does not seem to be so remote.

Alternatively, the pachyderms may have followed a horseshoe route from the northeastern Balkan areas southwards along the Adriatic shores of Italy (Sala 1990). This is the classical model, which however does not explain the absolute absence of *M. primigenius* and *C. antiquitatis* in central Italy as well as in most of the southern regions of the peninsula. The paleobiogeographic and paleogeographic settings seen so far lead to the conclusion that the Cardamone fauna is likely the result of a mixture of typical elements of the *Mammuthus-Coelodonta* faunal complex (*M. primigenius*, *C. antiquitatis*, *E. ferus* and *C. crocuta* probably immigrated from the east, along with red fox) with more temperate, autochthonous faunas (characterised, in particular, by *B. primigenius*, *C. elaphus*, *L. europaeus* and *O. cuniculus*). It apparently represents an ecotone connecting the cold Balkan bioprovince with the temperate Mediterranean and therefore suggests that Apulia formed a paleobioprovince somehow climatically and paleogeograpically connected with the Balkans. The combined absence of *E. hydruntinus* and *D. dama* may define the chronological position of this ecotone, since it is widely agreed that the two species were absent at the climax of the last glacial, that is at the second Würmian/ Weichselian Pleniglacial, which is dated some 22 - 18 ky before present.

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JAARBERICHT VAN HET NATUURMUSEUM ROTTERDAM

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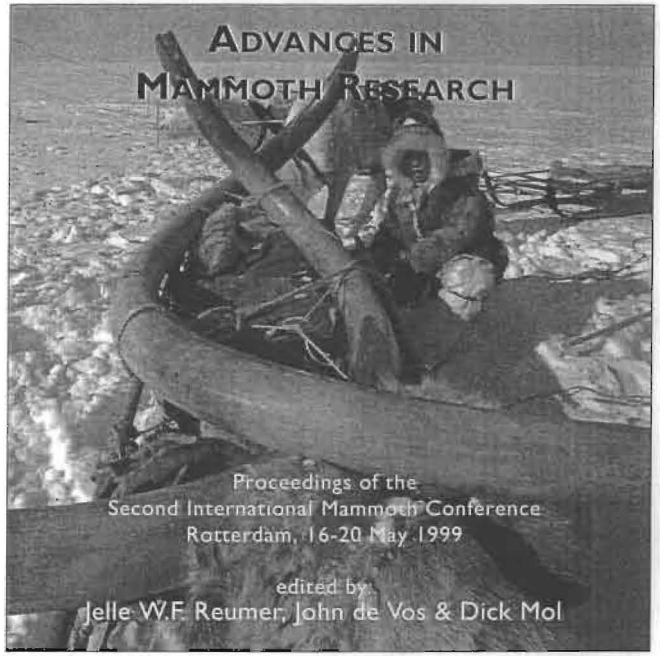

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